



ACOUSTIC BEHAVIOUR OF NORTHERN BOTTLENOSE WHALES (*HYPEROODON AMPULLATUS*) IN ICELANDIC INSHORE WATERS

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ABSTRACT

Northern bottlenose whales (*Hyperoodon ampullatus*) are among the deepest diving cetaceans, regularly foraging at depths >800 m. They are primarily found in offshore habitats, but occasionally they are also sighted within coastal waters. The drivers for these inshore movements remain unknown. Northern bottlenose whales use regular echolocation clicks and terminal ‘buzzes’ to find and capture prey, but they likely produce clicks for other functions like maintaining group cohesion. Between August and October 2022, a group of three northern bottlenose whales spent multiple weeks inshore within Eyjafjörður in northern Iceland. Here we quantify the acoustic signals attributed to the whales and describe their usage. Acoustic recordings were conducted on three days in late August and revealed the production of regular clicking and buzz-like rapid click trains. Click rates of rapid click trains were slower than those documented for northern bottlenose whale foraging buzzes and may instead have served a communication function. One animal among the group showed consistent unusual behaviour with prolonged logging at the surface; this animal washed ashore dead nine days later without fresh prey in its stomach. Thus, the group likely moved inshore seeking shelter and used echolocation for communication, though a navigational function cannot be ruled out.

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1. INTRODUCTION

Movement behaviour of whales is thought to be influenced by environmental factors and availability of resources. For instance, Norwegian killer whales (*Orcinus orca*) follow the seasonal migration of their herring prey from its inshore overwintering grounds to deeper offshore spawning grounds in spring and summer [1]. Prey-driven movement may also appear on shorter timescales; for example, short-finned pilot whales (*Globicephala macrorhynchus*) showed variations in their inshore-offshore movements and dive behaviour with solar and lunar cycles that correspond to the light-driven vertical movements of their prey [2]. Besides prey, the need for shelter also commonly drives movement behaviours. Mother-calf pairs of various cetacean species seek shallow water habitats as nursing grounds, offering mothers and their vulnerable offspring refuge from predators and male harassment [3–5]. Similarly, in delphinids the presence of predators has been shown to elicit short-term movements towards shore and into shallower waters [6].

The main distribution of northern bottlenose whales (*Hyperoodon ampullatus*), one of the better studied beaked whale species, is in offshore (sub-)polar waters of the North Atlantic [7–8] beyond the continental shelf and near submarine canyons and gorges [9]. This generally corresponds to the availability of their main prey, squid of the genus *Gonatus* [10], in search of which bottlenose whales perform hour-long, deep dives regularly reaching

depths of 400-1600 m [11-12]. Despite their primarily offshore distribution, they are also occasionally sighted within fjords and other coastal waters [13] but drivers for their inshore occurrence and movements remain unknown. The acoustic behaviour of northern bottlenose whales can shed light on broader behavioural aspects and habitat use. Their frequent production of echolocation clicks functions in orientation and prey detection during deep diving [14-17] but clicking has also been recorded during socialising at the surface [15, 18]. Hooker & Whitehead [15] described differences between clicks attributed to animals near the surface (*surface clicks*) opposed to *deep-water clicks* attributed to animals that were presumably foraging at depth. Deep-water clicks showed low variation in peak frequencies and ICIs, while surface clicks showed higher variation in both these parameters. Hooker & Whitehead [15] conducted their recordings at the surface, thus frequency differences between surface and deep-water clicks could have partially been driven by variations in the animals' orientation and distance to the hydrophone, and corresponding transmission loss and near-surface propagation effects [15].

Besides frequent clicking, rapid click trains called *buzzes* that follow regular search clicks play a crucial role in the final stage of prey capture for all odontocetes [19-20], including northern bottlenose whales [16]. By increasing the click rate, i.e. decreasing the ICI, the animals obtain a faster update of their prey's location and movement, aiding the capture of agile prey [21-22]. This functional use of buzzes is further supported by their temporal correlation with fast kinematic movements (northern bottlenose whales [12]; sperm whales (*Physeter macrocephalus*) [20]). Another type of rapid click trains called *rasps* has been described in Blainville's beaked whales (*Mesoplodon densirostris*) and these are thought to function in social communication and group coordination during deep dives [23]. While this sound type has been observed for northern bottlenose whales [24] a systematic description is lacking to date.

Between August and October 2022, a group of 3 northern bottlenose whales spent multiple weeks within Eyjafjörður, a long and narrow fjord in northern Iceland. To investigate potential drivers of their inshore movements and habitat use in coastal waters, we here quantify the acoustic signals attributed to the whales and describe their usage.

2. METHODS

Opportunistic acoustic recordings and concurrent ad libitum behavioural observations of a group of three northern

bottlenose whales were collected on three days in late August 2022. A total of 10 hours and 21 min were spent in the vicinity of the whales, which were confirmed to always be the same individuals by their scarring and skin lesions. On August 27th and 28th, the whales were encountered at the inland end of the fjord (65°40'38.9"N, 18°04'12.2"W) near the city of Akureyri. The fjord there forms an almost rectangular bay delimited largely by roads and the city's port. At its widest point, the bay area spans approximately 1.8 km and depths do not exceed 40 m. On these days, data were collected from aboard a rigid-hull inflatable boat (RHIB) or stand-up paddle board at distances between 30-500 m from the whales. On August 31st, the same group of three whales was encountered outside Hjalteyri (65°48'34.3"N, 18°09'21.9"W) close to shore where water depths ranged between 50-100 m. Acoustic recordings were conducted from the same RHIB at an approximate distance of 100-1000 m from the whales.

Acoustic data were collected using a 2-element vertical array with its two hydrophones (High Tech Inc, HTI-94-SSQ) connected to a handheld recorder (Tascam Portacapture X8). The hydrophones (including pre-amps) had a sensitivity of -165 dB re 1 V/ μ Pa and were located at depths of 15 and 20 m. Data were collected at a sampling frequency of 192 kHz. Recordings with the deeper hydrophone contained less noise from the surface than the shallower hydrophone and were thus used for further analysis (Raven Pro 1.6, Cornell Lab of Ornithology). A 5 kHz high-pass filter was applied to filter out low frequency noise and enhance signal to noise ratio.

Click trains were manually annotated based on visual and aural cues using a 20 s waveform and spectrogram (1024 NFFT, 60% overlap) display (Fig. 1). A new click train was defined to start after a period without clicks of at least 20 s. For calculations of ICIs, individual clicks were annotated in shorter, manually adjusted time windows of a few milliseconds long, using a waveform and high time resolution spectrogram (60 NFFT, 95% overlap) display (Fig. 2). ICIs were calculated as the time difference between the onset of two consecutive clicks. Regular click trains containing a minimum of 10 clicks were included in the analysis. ICIs exceeding 1 s were excluded to account for potential missed detections within a click train as this exceeds the maximum ICI of regular echolocation clicks reported in the current literature [14-17]. Clicks that were clearly visible in the spectrogram and had substantial spectral energy above the noise floor were selected for peak frequency measurements.

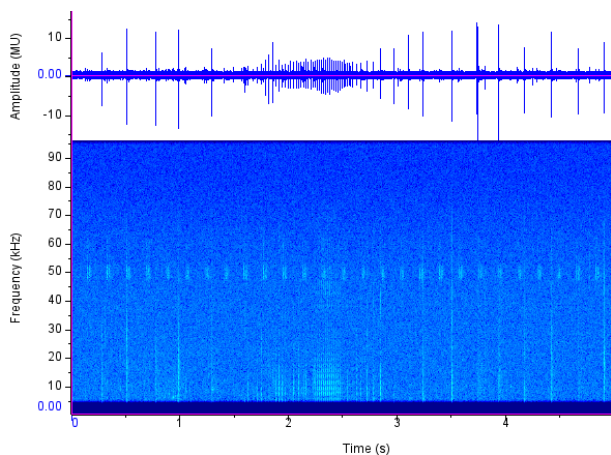


Figure 1. Waveform and spectrogram (1024 NFFT, 60% overlap) of northern bottlenose whale regular echolocation clicks interspersed with a rapid click train, and a 50 kHz echosounder in the background.

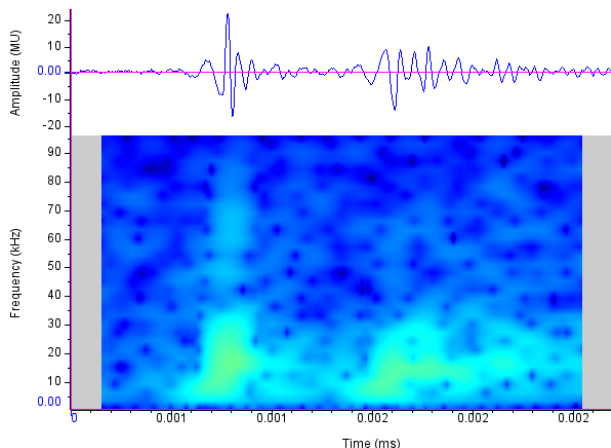


Figure 2. Waveform and spectrogram (NFFT 60, 95% overlap) of a recorded northern bottlenose whale regular click, followed by a reflection.

Rapid click trains were identified visually and aurally (Fig. 1), and all clicks with an ICI below 100 ms were considered part of the signal. To investigate whether these rapid click series constitute terminal buzzes, ICIs were calculated the same way as for regular clicking and clicks with substantial spectral energy were chosen for peak frequency measurements.

During acoustic data collection, ad libitum behavioural observations were conducted when the whales were at the surface. Notes including time stamps were taken on the

whales' overall behavioural state and specific events (e.g. spyhop, tailslap) while at the surface, their proximity to the hydrophone and the presence of other species and boats in the area. These were linked to acoustic detection times to ensure detected signals could be attributed to northern bottlenose whales.

3. RESULTS

Visual observations suggested that the group consisted of two adult females and one juvenile individual of unidentified sex (based on the species sexual dimorphism [25]). The behaviour of one non-juvenile whale, later confirmed to be an adult female, was consistently unusual with the animal spending prolonged periods of time logging at the surface while the other whales went on longer (up to 1 hour) dives more frequently. Whenever the seemingly distressed animal would go on a dive, it exhibited a stereotypical behaviour of repeated up and down bobbing before eventually having created sufficient momentum to fluke and dive. Nine days after the group has initially been sighted, this female washed ashore dead. Analysis of the animal's stomach content revealed that it had not fed in recent weeks, but the cause of death could not clearly be determined (F. Samarra, pers. comm.).

A total of 3 hours 50 minutes and 55 seconds of acoustic recordings were collected at estimated distances of 30-1000 m from the whales based on surface observations. Echolocation clicks were detected in 4.9% of the recorded data, spanning a total duration of 11 minutes and 16 seconds. Other cetacean species were not heard or seen during any of the recording periods and sounds produced by the whales could clearly be distinguished from anthropogenic sounds based on their frequency characteristics and timing. ICIs of regular echolocation clicks ($n=1172$ ICIs in 20 click trains) ranged from 38.5 to 977.7 ms with a mean of 265.0 ms (SD 139.6 ms). Peak frequencies of regular clicks had a mean of 17.7 kHz (SD 6.6 kHz, based on $n=444$ clicks from 16 click trains).

We identified 9 rapid click trains of which 6 were detected at sufficient amplitude to annotate individual clicks for ICI calculations. ICIs ($n=362$) in these click trains ranged from 13.3 to 96.4 ms with a mean of 26.7 ms (SD 13.0 ms). The measurable clicks within these rapid click trains had a mean peak frequency of 13.8 kHz (SD 4.3 kHz, based on $n=136$ clicks from 5 click trains). These statistics share similarities with previous findings [15-16] and unpublished data from two animal-attached sound and movement recording DTags deployed on northern bottlenose whales off Jan Mayen Island, Norway, in June 2014 and 2015 respectively (Tab. 1).

Table 1. Inter-click-intervals (ICIs) and peak frequencies of northern bottlenose whale clicks measured in this study (1 group, 3h 51min of recordings), compared to values reported by Hooker & Whitehead (15 groups, 7h 8min of recordings) [15] and Wahlberg et al. (1 group, 1h of recordings) [16], and ICIs of northern bottlenose whale rasps and buzzes from two DTag deployments (2 individuals in 2 groups, 25h 11min of recordings; unpublished data). *Peak frequency was measured on a subset of n=444 regular clicks and n=136 rapid clicks.

Type of click	Number of clicks	ICI mean \pm SD [ms]	Peak frequency mean \pm SD [kHz]	Location	Study
Regular	1172	265.0 \pm 139.5	17.7 \pm 6.6*	Inshore, Iceland	This study
Regular	856	306 \pm 118	-	Offshore, Faroe Islands	Wahlberg et al. [16]
Deep-water	52	400 \pm 50	23.88 \pm 1.71	Offshore, Canada	Hooker & Whitehead [15]
Surface	37	70 \pm 50	10.79 \pm 6.36	Offshore, Canada	Hooker & Whitehead [15]
Rapid	362	26.7 \pm 13.0	13.8 \pm 4.3*	Inshore, Iceland	This study
Buzz	469	8.4 \pm 1.3	-	Offshore, Faroe Islands	Wahlberg et al. [16]
Rasp	1684	29.5 \pm 14.1	-	Offshore, Jan Mayen, NO	DTag, unpublished
Buzz	4682	11.8 \pm 4.4	-	Offshore, Jan Mayen, NO	DTag, unpublished

4. DISCUSSION

The acoustic activity of northern bottlenose whales recorded in this study was comprised of regular echolocation clicks and rapid click series. ICIs of regular clicks spanned a great range and were most comparable to those reported by Wahlberg et al. [16] (Tab. 1). The presence of rapid click series in the recordings suggested that the animals used echolocation not solely for orientation, but also foraging or communication. While nearby concurrent fishing activity suggested potential prey availability, feeding was not visually observed, and rapid click series were emitted at a slower rate than has been reported for buzzes [16]. In comparison to unpublished data derived from two DTag deployments in offshore waters, mean ICIs within rapid click series recorded here matched those of rasps rather than buzzes (Tab. 1). Assuming that rasps serve a similar communication and group coordination function as has been suggested for Blainville's beaked whales [23], we suggest that the animals recorded here used sound for communication rather than foraging. However, a detailed description of acoustic properties and functional use of rasps in northern bottlenose whales is still lacking, limiting the interpretation of the results.

The hypothesis of the animals' acoustic activity functioning in communication is further supported by the circumstances of the encounter, given that one animal behaved in an aberrant fashion and later died. Shelter is a common driver for movements into coastal waters [3-6] and likely acted as such here. Reports from whalers indicate that northern

bottlenose whales typically stayed with injured animals until they died [26-27], thus the group might have moved into the fjord to accompany their sick conspecific, rather than following the movement of prey. Beyond the case study presented here, shelter could be a common driver for northern bottlenose whale's inshore movements. During the same period that the whales were present in Eyjafjörður, a group of 4 mother-calf pairs was seen repeatedly in the adjacent Skjálfandi Bay outside of Husavík (M. Glarou, pers. comm.), suggesting that the waters of North Iceland could constitute a refuge also for animals with vulnerable offspring. Moreover, a group of 6 northern bottlenose whales was encountered in Skjálfandi Bay in June 2022. Acoustic recordings of the group (13 min of data, recorded approx. 350 m from the whales) did not contain any clicks attributable to the animals, providing further evidence that the species might not be foraging extensively in these inshore waters. Shelter thus appears to be the more probable driver for northern bottlenose whale inshore movements in this case. However, more data from different years and locations are needed to confirm this pattern more broadly as the results and conclusions presented here stem from few observations and therefore must be considered as preliminary.

Peak frequencies of regular clicks were variable but on average lower than what has previously been reported for regular echolocation clicks produced during presumable foraging dives [14-15]. Rapid clicks were emitted with lower but similarly variable peak frequencies than regular clicks, making them more comparable to clicks recorded at the surface by Hooker & Whitehead [15] rather than those

assumed to be deep-water foraging clicks [14-15]. However, clicks recorded here in a shallow water environment are not readily comparable to recordings in deeper offshore waters. Different factors including source and receiver depth, reflection and refraction effects, sediment characteristics, and the local sound speed profile affect sound propagation [28]. The animal's orientation in relation to the hydrophone will further influence received frequency characteristics, particularly in species with high frequency and narrow beam pattern clicks as produced by northern bottlenose whales [16]. Knowledge on the animal's depth and position relative to the hydrophone, together with site-specific sound propagation modelling could help separate the effects of the environment and the sound source and provide deeper understanding of the differences between studies.

In conclusion, this study suggested that inshore movements of three northern bottlenose whales in North Iceland were more likely driven by shelter than prey availability. The frequency properties of described sounds differ from what is known for regular clicks in foraging dives [14-15] and rapid click series more closely resembled rasps, presumably functioning in communication, than terminal feeding buzzes [16]. Taken together with the absence of observed feeding behaviour or fresh prey in the stranded whales' stomach, we conclude that the animals used echolocation for communication rather than foraging. Though this conclusion must be considered preliminary due to the small sample size and a strict navigational function of the whales' clicks cannot be ruled out. A more thorough understanding of the species' acoustic repertoire and use of sound would be necessary to derive more conclusive inferences from acoustic behaviour on habitat use and should be the focus of future research.

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6. REFERENCES

- [1] E. F. Vogel et al., "Killer whale movements on the Norwegian shelf are associated with herring density," in *Mar Ecol Prog Ser*, vol. 665, pp. 217–231, 2021.
- [2] K. Owen, R. D. Andrews, R. W. Baird, G. S. Schorr, and D. L. Webster, "Lunar cycles influence the diving behavior and habitat use of short-finned pilot whales around the main Hawaiian Islands," in *Mar Ecol Prog Ser*, vol. 629, pp. 193–206, 2019.
- [3] S. H. Elwen and P. B. Best, "Female southern right whales *Eubalaena australis*: Are there reproductive benefits associated with their coastal distribution off South Africa?," in *Mar Ecol Prog Ser*, vol. 269, pp. 289–295, 2004.
- [4] J. S. Weir, N. M. T. Duprey, and B. Würsig, "Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: Are shallow waters a refuge for nursery groups?," in *Can J Zool*, vol. 86, no. 11, pp. 1225–1234, 2008.
- [5] A. S. Craig, L. M. Herman, A. A. Pack, and J. O. Waterman, "Habitat segregation by female humpback whales in Hawaiian waters: Avoidance of males?," in *Behaviour*, vol. 151, no. 5, pp. 613–631, 2014.
- [6] M. Srinivasan, "Predator/Prey Decisions and the Ecology of Fear," in *Ethology and Behavioral Ecology of Odontocetes*, B. Würsig, Ed., Cham: Springer International Publishing, pp. 145–163, 2019.
- [7] C. D. MacLeod and A. D'Amico, "A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise," in *J Cetacean Res Manage*, vol. 7, no. 3, pp. 211–221, 2006.
- [8] H. Whitehead and S. K. Hooker, "Uncertain status of the northern bottlenose whale *Hyperoodon ampullatus*: Population fragmentation, legacy of whaling and current threats," in *Endang Species Res*, vol. 19, no. 1. Inter-Research, pp. 47–61, 2013.
- [9] T. Wimmer and H. Whitehead, "Movements and distribution of northern bottlenose whales, *Hyperoodon ampullatus*, on the Scotian Slope and in adjacent waters," in *Can J Zool*, vol. 82, pp. 1782–1794, 2004.
- [10] S. K. Hooker, S. J. Iverson, P. Ostrom, and S. C. Smith, "Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy



- samples,” in *Can J Zool*, vol. 79, no. 8, pp. 1442–1454, 2001.
- [11] S. K. Hooker and R. W. Baird, “Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae),” in *Proc R Soc B*, vol. 266, pp. 671–676, 1999.
- [12] E. Siegal, “The foraging behaviour and body condition of northern bottlenose whales (*Hyperoodon ampullatus*),” doctoral dissertation, University of St Andrews, St Andrews, 2020.
- [13] T. Grove, C. Senglat, M. Petitguyot, D. Kosiba, and M. H. Rasmussen, “Mass stranding and unusual sightings of northern bottlenose whales (*Hyperoodon ampullatus*) in Skjálfandi Bay, Iceland,” in *Mar Mamm Sci*, vol. 36, no. 3, pp. 1033–1041, 2020.
- [14] E. Clarke, L. J. Feyrer, H. Moors-Murphy, and J. Stanistreet, “Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*) and Sowerby’s beaked whales (*Mesoplodon bidens*) off eastern Canada,” in *J Acoust Soc Am*, vol. 146, no. 1, pp. 307–315, 2019.
- [15] S. K. Hooker and H. Whitehead, “Click characteristics of northern bottlenose whales (*Hyperoodon ampullatus*),” in *Mar Mamm Sci*, vol. 18, no. 1, pp. 69–80, 2002.
- [16] M. Wahlberg, K. Beedholm, A. Heerfordt, and B. Møhl, “Characteristics of biosonar signals from the northern bottlenose whale, *Hyperoodon ampullatus*,” in *J Acoust Soc Am*, vol. 130, no. 5, pp. 3077–3084, 2011.
- [17] B. Martin and H. Moors-Murphy, “Analysis of northern bottlenose whale pulses and associated reflections recorded from the Gully Marine Protected Area,” in *Proc Mts Acoust*, 2013.
- [18] H. B. Moors-Murphy, “Patterning in northern bottlenose whale (*Hyperoodon ampullatus*) click trains,” in *Canadian Acoustics*, vol. 43, no. 3, 2015.
- [19] M. Johnson, P. T. Madsen, W. M. X. Zimmer, N. Aguilar De Soto, and P. L. Tyack, “Foraging Blainville’s beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation,” in *J Exp Biology*, vol. 209, no. 24, pp. 5038–5050, 2006.
- [20] P. J. O. Miller, M. P. Johnson, and P. L. Tyack, “Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture,” in *Proc R Soc B*, vol. 271, no. 1554, pp. 2239–2247, 2004.
- [21] P. T. Madsen and A. Surlykke, “Echolocation in Air and Water,” in *Biosonar*, A. Surlykke, P. E. Nachtigall, R. R. Fay, and A. N. Popper, Eds., Springer-Verlag New York, pp. 257–304, 2014.
- [22] H. Vance et al., “Echolocating toothed whales use ultra-fast echo-kinetic responses to track evasive prey,” in *Elife*, vol. 10, 2021.
- [23] N. Aguilar de Soto et al., “No shallow talk: Cryptic strategy in the vocal communication of Blainville’s beaked whales,” in *Mar Mamm Sci*, vol. 28, no. 2, pp. E75–E92, 2012.
- [24] P. J. Wensveen et al., “Northern bottlenose whales in a pristine environment respond strongly to close and distant navy sonar signals,” in *Proc R Soc B*, vol. 286, 20182592, 2019.
- [25] S. Gowans, M. L. Dalebout, S. K. Hooker, and H. Whitehead, “Reliability of photographic and molecular techniques for sexing northern bottlenose whales (*Hyperoodon ampullatus*),” in *Can J Zool*, vol. 78, pp. 1224–1229, 2000.
- [26] T. Benjaminsen and I. Christensen, “The Natural History of the Bottlenose Whale, *Hyperoodon ampullatus* (Forster),” in *Behaviour of Marine Animals*, Boston, MA: Springer US, pp. 143–164, 1979.
- [27] D. Gray, “Notes on the Characters and Habits of the Bottlenose Whale (*Hyperoodon rostratus*),” in *Proc Zool Soc London*, vol. 50, no. 4, pp. 726–731, 1882.
- [28] W. W. L. Au and M. C. Hastings, *Principles of Marine Bioacoustics*. New York, NY: Springer US, 2008.